

Taxonomic occurrences of gastropod spermatozuigmata and non-stylommatophoran spermatophores updated

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Abstract: Spermatozuigmata, not to be confused with spermatophores, that also transfer sperm, are compound structures (parasperms with attached eusperms) known only in certain “mesogastropods”: Loxonematoidea? (Abyssochrysidae), Littorinoidea (Littorinidae), Triphoroidea (Triphoridae and Cerithiopsidae), Tonnoidea (Ranellidae), Janthinoidea (Epitoniidae and Janthinidae), and doubtfully Cypraeoidea (Cypraeidae). This pattern of taxonomic occurrence does not match that of any other character known, their morphology is diverse, and it is concluded that the spermatozuigmata in these taxa are not all homologous and that, like spermatophores, they have evolved repeatedly. Littorinid spermatozuigmata have frequently been studied after fixation and shrinkage of the parasperms (“nurse cells”), during which the eusperms drop off. Spermatozuigmata are not a synapomorphy linking the Triphoroidea and Janthinoidea. Records of spermatophores (except in the “pulmonate” suborder Stylommatophora) since Robertson (1989) are updated.

Key words: sperm transfer, inferred homoplasy, euspermatozoa, paraspermatozoa, nurse cells

SPERMATOZEUGMATA

Spermatozuigmata (singular: spermatozuigma) are not to be confused with spermatophores (Robertson 1989) although both transfer sperm. Spermatozuigmata are of intracellular origin and consist of single paraspermatozoa (Hodgson 1997, Buckland-Nicks *et al.* 2000) with numerous euspermatozoa (fertile sperm) attached externally by their acrosomes. Parasperm are also called apyrene sperm and nurse cells. They are known only in “prosobranchs”, but do not all become spermatozuigmata. Spermatophores are secreted extracellularly and contain the eusperms. Spermatophores occur sporadically in many major groups within all gastropods, including many stylommatophorans. Spermatozuigmata are even more sporadic and are known only in certain “mesogastropods”:

Incertae sedis (Loxonematoidea?): Abyssochrysidae: *Abyssochrysos* (Healy 1989).

Littorinoidea: Littorinidae: *Littoraria* (Reinke 1911, as “*Littorina*”), *Littorina*, *Littoraria* (Reinke 1912, latter as “*Littorina*”), *Littorina* (Ankel 1930: 599, 600; Linke 1933), *Littoraria* (Woodard 1942a, 1942b, Lenderking 1954, all as “*Littorina*”, latter: nurse cell as “spermatophore”), *Melarhaphe* (Battaglia 1952, as “*Littorina*”), *Littoraria* (Marcus and Marcus 1963, as “*Littorina*”), *Bembicium* (Bedford 1965), *Cenchritis* (as “*Tectarius*”), *Tectarius* (as “*Echinium*”), *Littoraria* (as “*Littorina*”), *Nodilittorina* (in part as “*Littorina*” (all Borkowski 1971), *Littorina* (Buckland-Nicks 1973, Buck-

land-Nicks and Chia 1977), *Nodilittorina* (Jordan and Ramorino 1975, as “*Littorina*”), *Littoraria* (Reid 1986, Healy and Jamieson 1993, Buckland-Nicks *et al.* 2000).

Triphoroidea [including “Cerithiopsidae”]: Triphoridae: *Triphora* (Houston 1985), *Viriola* (Healy 1987, 1990). Cerithiopsidae: *Cerithiopsis* (Fretter and Graham 1962, Houston 1985), *Seila* (Houston 1985, Healy 1990).

Cypraeoidea?: Cypraeidae?: *Erronea*? (Healy 1986a, as “*Cypraea*”).

Tonnoidea: Ranellidae: *Fusitriton* (Buckland-Nicks *et al.* 1982).

Janthinoidea [“Epitonioidae”]: Epitoniidae: *Epitonium* (Ankel 1926, 1938: 6-9, 1958, all as “*Scala*”, Fretter 1953, as “*Clathrus*”), *Opalia* (Bulnheim 1962a, 1962b), *Epitonium* (Nishiwaki 1964, Tochimoto 1967, Bulnheim 1968, Nishiwaki and Tochimoto 1969), *Opalia*, *Epitonium* (Melone *et al.* 1978, 1980, latter as “*Scala*”), *Epitonium* (Robertson 1983a, 1983b, Collin 2000, as “*Nitidiscala*”). Janthinidae: *Janthina* (Ankel 1926, 1930, Laursen 1953, Graham 1954, Wilson and Wilson 1956, as “*Ianthina*”). Curiously, two epitoniid species have dimorphic spermatozuigmata (Nishiwaki and Tochimoto 1969).

The all-“mesogastropod” taxonomic pattern of occurrence of spermatozuigmata is non-congruent with any other character known. Robertson (1985, 1989: table 1) and Collin (1997, 2000) reported the congruent occurrences of up to five non-homologous characters, suggesting that the taxa are related. The non-congruence of spermatozuigmata and their varied morphologies suggest that they are not homologous between the superfamilies listed above. The same descriptive name in different taxa does not make a character homolo-

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gous. The compound origin and nature of spermatzeugmata could well have originated by homoplasy. The Triphoridae appear to have both spermatzeugmata and spermatophores, perhaps in different genera, but this needs confirmation.

The distinctive nurse cells of littorinids are believed to be parasperms. They are characteristic in being spherical to oblong, with or without projecting rods. In the *Littoraria* subgenus *Palustorina* the nurse cells are elongate or fusiform, having a pseudotrich. Reid has not seen and reported attached eusperms since 1986, perhaps because since then he has consistently studied littorinid parasperms after fixation and shrinkage. As Reinke (1912), Woodard (1942b), Marcus and Marcus (1963), Jordan and Ramorino (1975), and Healy and Jamieson (1993) have observed, the acrosomes are attached weakly and the eusperms drop off easily. Perhaps all littorinids have these evanescent "spermatzeugmata". A cypreaid (*Erronea*) appears to have dimorphic parasperms: vermiform ones as well as spherical, littorinid-like "nurse cells." Eusperms are semi-attached only to the latter, and these "could be considered a form of 'spermatzeugmata'" (Healy 1986a).

Healy (1987) stated that the spermatzeugmata of *Virolia* (Triphoridae) are "very mobile", but in 1990 he stated that they and those of *Seila* (Cerithiopsidae) are "capable of only slow movement." Original observations on the behavior of living janthinoidean spermatzeugmata are included in Wilson and Wilson (1956), Nishiwaki and Tochimoto (1969), Melone *et al.* (1980), and Robertson (1983a). Uniformly, there seems to be pseudocopulation. They are not "vigorously mobile," swimming with "considerable speed" on their "relatively long journeys."

Fretter (1953), Healy (1986b, 1987, 1990, 1994), and Nützel (1998) believed that because of their spermatzeugmata the Triphoridae and Cerithiopsidae are related to the Janthinoidea. They are similar in being large and containing numerous axonemes, but otherwise they are morphologically different in the three groups. Nützel (1998: 2) went so far as to suggest that spermatzeugmata are the "most convincing synapomorphy." Overlooking Nützel's monograph, Collin (2000) reviewed most of the characters traditionally used to support the "Ptenoglossa" (including the Eulimidae but excluding the Architectonicidae, neither of which has known spermatzeugmata). There appear to be no other possible synapomorphies. Other literature on the Triphoroidea and Janthinoidea bears this out: Pruvot-Fol (1925, 1952), Johansson (1947, as "*Scala*", 1953), Risbec (1953), Graham (1954), Marcus and Marcus (1963), Houston (1985), Houbbrick (1987), and Collin (2004). "Ptenoglossan" radulae are diverse morphologically. If there is only one supposed "synapomorphy" linking two superfamilies, the validity of it may be questioned. Thus, I agree with Ponder

(1998) that it is improbable that Triphoroidea and Janthinoidea are closely related.

SPERMATOPHORES

Records in non-stylommatophorans since Robertson (1989):

Neritoidea: Neritiliidae: *Pisulina* (Kano and Kase 2002), *Neritilia* (Kano *et al.* 2001, Kano and Kase 2003). Neritidae: *Clithon*, *Neritina* [as "*Neripteron*" and "*Vittina*"] (Starmühlner 1970), *Neritina*, *Septaria* (Starmühlner 1974), *Clithon*, *Neritina*, *Septaria* (Starmühlner 1976), *Clithon*, *Neritina* (Starmühlner 1983, 1984), *Nerita*, *Neritilia*, *Neritina*, *Puperita* (Starmühlner 1988), *Septaria* (Haynes and Wawra 1989), *Nerita*, *Neritina* (Houston 1990), *Theliostyla* (Zehra and Perveen 1991), *Nerita*, *Puperita*, *Clithon*, *Neritina*, *Septaria*, *Neritilia* (Starmühlner 1993), *Nerita* (Sasaki 1998), *Septaria* (Haynes 2001), *Septaria*, *Neritina* (Haynes 2005). Phenacolepadidae: *Cinnulepeta*? (Sasaki 1998).

Campaniloidea: Plesiotrochidae: *Plesiotrochus* (Houbbrick 1990). [Placement: Healy 1993].

Cerithioidea: Cerithiidae: *Bittium*? *Bittiolium* (Houbbrick 1993), *Cerithium* (Houbbrick 1992). Dialidae?: *Diala*? (Ponder 1991). Melanopsidae (as "Thiaridae; Melanopsinae"): *Faunns* (Houbbrick 1991b). Paludomidae (including Thiaridae, *s. l.*): *Lavigeria* (Michel 1995), *Tanganyicia* (West 1997, Strong and Glaubrecht 2002), *Tiphobia*, *Paramelania*, *Limnotrochus*, *Chytra*, *Tanganyicia*, *Stanleya*, *Mysorelloides*, *Reymondia*, *Lavigeria*, *Spekia*, *Stormsia* (Glaubrecht and Strong 2004). Pleuroceridae: *Elimia* (Jones and Branson 1964, as "*Mudalia*"), *Semisulcospira* (Nakano and Nishiwaki 1989). Potamididae: *Terebralia* (Houbbrick 1991a). Scaliolidae: *Finella* (Ponder 1994). Thiaridae, *s. l.*: *Vinundu* (Michel 2004). Thiaridae, *s. s.*: *Thiara* (Glaubrecht and Strong 2004). Turritellidae: *Turritella* (Kennedy 1995).

Pterotracheoidea: Atlantidae: *Atlanta* (Jamieson and Newman 1989). Carinariidae: *Pterosoma* (Lalli and Gilmer 1989). The "spermatophores" in Atlantidae reported by Tesch (reference in Robertson 1989) are actually the egg cases of a pleustonic insect, *Halobates* (Seapy 1996).

Vermetoidea: Vermetidae: *Dendropoma*, *Serpulorbis*, *Vermetus* (Calvo and Templado 2005).

Pyramidelloidea: Pyramidellidae: *Pyramidella*? (Ponder 1987), *Boonea* (Wise 2001), *Fargoa* (Robertson 1996), *Iolaea* (Hori and Kuroda 2001), *Odostomella* (Schander *et al.* 1999), *Parthenina* (Hori and Kuroda 2002).

Cavolinioidea: Cavoliniidae: *Diacria* (Lalli and Gilmer 1989). Limacinidae: *Limacina* (Lalli and Gilmer 1989).

Clionoidea?: Pneumodermatidae?: *Crucibranchaea*? (Lalli and Gilmer 1989).

Hedylopoidea: Parhedylidae: *Pontohedyle*, *Unela* (Poizat 1989).

Aeolidioidea: Aeolidiidae: *Aeolidiella* (Haase and Karlsson 2000).

Spermatophore presence can be difficult to ascertain, and a "spermatophore bursa" in a pallial oviduct may not always receive one (despite my assumption to the contrary in 1989: 362, A7). In Robertson (1989) I reported spermatophores in the cerithioidean Litiopidae, but Houbrick observed only bursae in them. Glaubrecht and Strong (2004) inferred the spermatophore-forming organ in male paludomid cerithioideans.

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